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Phytotoxic Potential of Gambel Oak on Ponderosa Pine Seed Germination and Initial Growth

Michael G. Harrington



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Abstract

Water soluble leachates from Gambel oak leaves reduced speed of germination and initial radicle growth of ponderosa pine seeds in laboratory and greenhouse experiments. The combined effects of Gambel oak competition and allelopathy are implicated as contributing factors limiting natural regeneration of ponderosa pine in many forest stands in the Southwest.

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Management Implications

Natural ponderosa pine regeneration in the Southwest generally is difficult because of long dry periods, frost heaving, active rodent populations, deep organic seedbeds, and competition with vigorous grasses and shrubs. Also, allelopathy may be actively involved, as indicated by pine exclusion from pine-bunchgrass communities (Rietveld 1975).

This research implicates Gambel oak as a possible producer of phytotoxins which, together with competition, may retard growth of ponderosa seedlings, making them more susceptible to other environmental stresses. If this is happening, site preparation for natural ponderosa regeneration is essential. Long-term planning is necessary to manage sites with oak understories, because Gambel oak is a vigorous sprouter and very difficult to control. Because herbicides at environmentally safe levels are generally ineffective, and root plowing in existing ponderosa pine stands is impractical, site preparation by prescribed burning is recommended. Midsummer, fire application at 2-year intervals will reduce Gambel oak coverage and density, while preparing a receptive seedbed for natural ponderosa pine regeneration (Harrington 1985).

Introduction

Gambel oak (*Quercus gambelii*) is found on about 3.5 million hectares in the West, much of which lies within the ponderosa pine (*Pinus ponderosa*) zone (Harper et al. 1985). Because oak and pine frequently occupy the same sites, competition between them is expected (DeVelice et al. 1986, Harper et al. 1985). Many sites which once were occupied by ponderosa pine are now Gambel oak brushfields and many ponderosa pine stands with dense oak understories have had little natural pine regeneration in the last few decades.² Competition for limited resources is thought to be the primary cause of this lack of natural regeneration. Historically, frequent fires helped to maintain ponderosa pine stands by seedbed preparation and competition control (Weaver 1951, Cooper 1960). These benefits have been eliminated with the recent effective suppression of natural wildfires. Chemical inhibition of ponderosa pine by Gambel oak could also influence regeneration. Plant chemical interactions are frequently suspected in regeneration failures (Fisher 1980).

The purpose of this research was to determine if natural plant products of Gambel oak leaves, litter, and duff are potentially toxic to ponderosa pine, reducing seed germination and initial seedling growth, and ultimately suppressing natural regeneration.

Literature Review

Allelopathy, the adverse chemical effect of one plant on another, is considered a universal phenomenon (Rice 1974). It differs from competition in that it involves placement of natural chemicals into the environment, whereas competition involves the rivalry for growth requirements, such as light, water, and nutrients (Rietveld 1979).

Many studies have shown the presence of chemical interactions between plants in agriculture; but reports from forest communities are less common. McPherson and Thompson (1972) found that understory species were suppressed with both physical and chemical actions by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*). Lodhi (1976) found that soils under hackberry (*Celtis* spp.), sycamore (*Plantus occidentalis*), red oak (*Quercus rubra*), and white oak (*Q. alba*) produced consistent phytotoxic inhibition of understory species.

Conifers are also involved in chemical interaction. Broomsedge (*Ardropogon virginicus*) can inhibit seed germination and seedling growth of loblolly pine (*Pinus taeda*) (Priester and Pennington 1978). Seed germination and/or initial growth of jack pine (*Pinus banksiana*) and red pine (*P. resinosa*) were reduced by natural chemicals from associated vegetation (Brown 1967, Norby and Kozlowski 1980). Del Moral and Cates (1971) found that extracts from various shrubs and forbs inhibited radicle growth of Douglas-fir (*Pseudotsuga menziesii*). Ponderosa pine seed germination and growth were greatly reduced by extracts from Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) (Rietveld 1975), as well as from Utah juniper (*Juniperus osteosperma*) (Jameson 1968). Many species of oak produce allelopathic effects. Rietveld's (1979) review lists eight oak species which retard the growth of associated vegetation, by chemical inhibitions alone or in combination with competition. Tannins and other water soluble phenolics, which are common in oak foliage, are thought to be important allelochemicals (Feeny 1970, Taylor and Shaw 1983). Gambel oak leaves, acorns, and litter contain sufficient quantities of tannins to sicken and kill cattle (USDA 1968).

In vegetative types where fire has been common, it may have inactivated toxic plant substances, encouraging regeneration. Went et al. (1952) and Christensen and

²Steinhoff, H. W. Gambel oak ecology. District Office Report. Colorado State University, Durango, CO. 1981. 5 p.

Muller (1975) report that this process is active in chaparral. Indirect evidence suggests fire may benefit jack pine in this way also (Brown 1967). Rietveld (1979) states that seed germination and growth may be chemically inhibited in many forest seedbeds with heavy litter accumulation. This could help to explain why some species, such as ponderosa pine, regenerate much more readily where fire has exposed mineral soil seedbeds.

No record of Gambel oak allelopathy could be found. However, its suppression of herbaceous vegetation on rangeland, presumably by competition for moisture and light, is well documented (Moinat 1956, Jefferies 1965, Marquiss 1973). Marquiss (1969) and Tew (1969) report increases in available soil moisture following oak control. In forests or oak brushfields which were once forests, the occurrence of Gambel oak frequently coincides with a distinct absence of ponderosa pine regeneration² (Pearl 1965). Competition for moisture again is suspect.

Methods

Gambel oak plant materials were collected from a ponderosa pine-Gambel oak site in southwestern Colorado, on the San Juan National Forest. Plant parts used were green leaves of mature oaks, green leaves of 1-year-old oak sprouts, newly fallen oak litter, and well-decomposed oak duff. Ponderosa pine seeds used in all experiments were collected from the same site.

Before the experiment began, the pine seeds were surface-sterilized with a 10-minute soak in 30% hydrogen peroxide. During the experiments, germination counts were made daily. Germination was assumed when the emerging radicle equalled the seed coat in length. The first five germinants in each replication were allowed to grow for 5 days, at which time the radicle lengths were measured. The rest of the seeds were discarded as they germinated. Experiments were terminated when germination had ceased for 1 week. Most experiments lasted for 18 to 24 days.

Experiment 1

This experiment tested the direct effect of oak leaves, litter, and duff on ponderosa pine seed germination and radicle growth.

Two grams of one of the following oak materials was placed in each of five, 9-cm petri dishes: mature oak leaves, sprout leaves, litter, and duff. Oak material was broken in small pieces, but was not ground. Coarse tissue paper was used in the control treatment. A sheet of fiberglass filter paper was placed on top of the plant materials and tissue. Fifty pine seeds were put on the filter paper, and each dish was moistened with 10 ml of distilled water. Moisture from the wet plant material easily leached through the filter paper, contacting the seeds. All dishes were randomly placed in a growth chamber set for 12 hours at 25 °C and 70% relative humidity with light and 12 hours at 18 °C and 90%

relative humidity in darkness. The oak and tissue material was remoistened as needed.

Experiment 2

This experiment tested the phytotoxic effect of Gambel oak leachates on ponderosa pine seed germination and radicle growth.

Leachates were prepared with each of the four oak materials by placing 100 g oven dry equivalent of fresh plant material in 1 l of distilled water, stirring for 10 minutes, and allowing to set overnight. The solid material was filtered out, and the leachates were stored at 2 °C until needed.

Because the pH and the osmotic potential of a solution can affect germination and initial growth, these qualities of each leachate were measured. The osmotic potentials were determined using thermocouple psychrometers. All were greater (less negative) than -1.0 bar and, therefore, should not have affected germination and growth differently than a distilled water control at 0.0 bars (Rietveld 1975). The pH of the oak leachates ranged from 4.1 for litter to 6.3 for duff. To test the possible effect of low pH, a control with pH of 4.0 was prepared using hydrochloric acid and distilled water.

Fiberglass filter paper and 50 ponderosa pine seeds were placed in each of 30, 9-cm petri dishes. Three ml of one of the four leachates, the pH control, or distilled water were pipetted into each of five dishes. All dishes were randomly placed into a growth chamber set at the same condition as Experiment 1. Seeds were remoistened as needed. The filter papers were changed every 2-3 days to reduce possible concentration of chemicals.

Experiment 3

This experiment tested the effects of ponderosa pine seed exposure to a simulated overwintering period in Gambel oak plant leachates.

Leachates of mature oak leaves, sprout leaves, fresh litter, and oak duff were prepared as in Experiment 2. Fifty ponderosa pine seeds were placed between two sheets of fiberglass filter paper in each of 30, 9-cm petri dishes. One plant leachate, pH control, or distilled water control was added to each of five dishes. The dishes were stored in a refrigerator set at 2 °C. The filter papers were remoistened periodically and replaced monthly. After 3 months, the seeds were placed on clean filter papers in new petri dishes, moistened with 3 ml of distilled water, and placed in a growth chamber set at the same condition as in Experiment 1.

Experiment 4

This experiment tested the effects of Gambel oak leachates on ponderosa pine seed emergence and seedling growth in forest soils.

Large quantities of the same four oak materials previously used were brought to a greenhouse and dried

for 2 weeks. Soil was also collected from the same pine-oak site. The soil was taken from the upper 6 inches of a forest opening, where no oaks or pines were growing, to avoid any residual influence. The soils were brought to the greenhouse, sifted to remove stones, and placed in plastic pots (18 cm high x 15 cm wide).

Twenty ponderosa pine seeds were planted 1 cm deep in each of 35 pots. Oak leachates were prepared as needed by mixing 200 g of air-dry, unbroken plant material in 2 l of tap water. The mixture was allowed to set overnight, and then all solid material was filtered out. Seven pots each were watered with 200 ml of either one of the leachates or tap water (control). Rewatering took place as needed, usually weekly during seedling emergence and, later, biweekly.

Germination or, in this case, emergence was checked daily until complete. Three weeks after emergence started, each pot was thinned to five seedlings, which were allowed to grow with infrequent watering with the respective leachates or tap water. Greenhouse temperatures most commonly ranged from 15 °C to 30 °C and relative humidity from 40% to 90%. When the seedlings were about 4 months old, they were removed from the pots by washing away the soil. Seedling crown lengths were measured. The root systems were so greatly branched because of contact with the bottom and sides of the pots that measurement of individual root lengths was considered meaningless. However, the shoot and root weights were determined after oven drying at 70 °C for 24 hours.

Analysis

Total germination (emergence) and speed of germination (emergence) (Maguire 1962) between treatments were tested with analysis of variance followed by Tukey's test, if differences were indicated at the 5% level. Because more than one seedling per dish or pot was used for radicle lengths, crown height, and shoot and root weights, a nested-design analysis of variance was used to compare treatment means. Tukey's test then was used for individual treatment comparisons.

Results

The ponderosa pine seeds collected in 1983 that were used in these experiments were highly viable. With total germination in all four experiments ranging from 89% to 99%, no significant differences were found.

In Experiment 1, total germination ranged from 96.0% in the controls to 88.8% in sprout leaves with no adverse effects shown. However, significant differences were found in speed of germination and 5-day radicle length (table 1). Speed of germination was reduced by about 25% by both leaf treatments. In addition, mature oak leaves reduced pine radicle growth by about 40%, and sprout leaves slowed growth by about 55% of controls.

In Experiment 2, total germination again was nearly complete, reaching a high of 99.2% in distilled water con-

trols and down to 97.6% in the duff leachate. Speed of germination was about 33% faster in the controls than in both green leaf and the litter leachates, and radicle lengths were 25% shorter, again in the green leaf extracts (table 2).

In Experiment 3, pine seeds that experienced a 3-month simulated overwintering period had excellent germination regardless of treatment, ranging from 98.4% for the controls to 92.8% for the mature oak leaf leachate. Table 3 shows that both speed of germination and radicle growth were affected by "overwintering" in certain leachates. Litter and mature leaf leachates slowed germination 16% and 12%, respectively. "Overwintering" in mature leaf leachates also reduced radicle growth by about 32% of the distilled water control, while sprout leaf leachates reduced radicle growth by 17%.

In Experiment 4, pine seedling emergence from forest soils was excellent again, ranging from 96.4% for the mature leaf treatment to 94.3% for the duff treatment. In contrast to the other experiments, speed of emergence was similar in all treatments, with the controls being the most rapid at 1.5 seeds per day and the litter treatment being the slowest at 1.3 seeds per day. However, because emergence from soil in pots is much slower than germination in petri dishes, the calculated speed of emergence values are very low and possibly misleading. Another commonly used emergence rate indicator, which probably is more applicable here, is days to 50% emergence. These values (table 4) indicate that seedlings watered with leaf leachates took about 2 days longer to emerge than those with tap water. Figure 1 also shows that from days 12 to 16, emergence in the controls was 2 to 3 days ahead of that in both leaf leachate treatments. Table 4 also compares crown heights, and shoot and root weights of seedlings grown 4 months in each treatment. No significant differences were found.

Discussion and Conclusions

The results from Experiments 1, 2, and 3 indicate that water soluble substances with allelopathic potential towards ponderosa pine occur in Gambel oak foliage. Total germination was not reduced by any treatments; but both speed of germination and initial seedling radicle growth were. Two explanations for this are possible. First, substances leached from the oak materials may simply not inhibit the initiation of germination. Second, potentially toxic substances may be incapable of penetrating an unbroken pine seed coat because of large molecular size. However, in either case, once the seed coat opens because of swelling, the substances contacted the germinating embryo, slowing the process. Because germination was not considered complete until the radicle equalled the length of the seed coat, speed of germination was reduced. However, the radicle eventually reached the minimum length, completing germination. Neither pH nor osmotic potentials were different enough from the distilled water controls to cause any of the adverse effects.

In both Experiments 1 and 2, germination speed and radicle lengths were reduced in the presence of oak

Table 1.—Effects of mature oak leaves, sprout leaves, litter, and duff of Gambel oak on speed of germination and 5-day radicle growth of ponderosa pine (Experiment 1).

Treatment	Speed of germination (seeds/day)	Radicle length (mm)
Mature leaves	5.1 a ¹	25.7 a
Sprout leaves	5.4 a	18.8 a
Litter	7.5 b	49.2 c
Duff	6.9 b	41.1 b
Control (tissue paper)	6.9 b	42.4 bc

¹Values followed by different letters are significantly different at the 5% level.

Table 2.—Effects of water soluble leachates of Gambel oak mature leaves, sprout leaves, litter, and duff on speed of germination and 5-day radicle growth of ponderosa pine (Experiment 2).

Treatment	Speed of germination (seeds/day)	Radicle length (mm)
Mature leaves	4.4 a ¹	26.1 a
Sprout leaves	4.4 a	27.6 a
Litter	4.4 a	34.0 bc
Duff	5.9 b	32.1 b
pH control	6.7 b	34.0 bc
Control (distilled water)	6.3 b	36.8 c

¹Values followed by different letters are significantly different at the 5% level.

Table 3. Effects of overwintering simulation in Gambel oak leachates from mature oak leaves, sprout leaves, litter, and duff on ponderosa pine germination speed and 5-day radicle growth (Experiment 3).

Treatment	Speed of germination (seeds/day)	Radicle length (mm)
Mature leaves	5.0 a ¹	21.7 a
Sprout leaves	5.5 ab	26.2 b
Litter	4.7 a	30.4 c
Duff	6.2 bc	30.1 bc
pH control	7.1 c	30.5 c
Control (distilled water)	5.7 b	31.7 c

¹Values followed by different letters are significantly different at the 5% level.

Table 4. Effects of leachates of Gambel oak mature leaves, sprout leaves, litter, and duff on emergence and growth of ponderosa pine seedlings in forest soils (Experiment 4).

Treatment	Days to 50% germination (number of days)	Crown length (mm)	Shoot weight (g)	Root growth (g)
Mature leaves	13.7 a ¹	50.8 a	0.28 a	0.30 a
Sprout leaves	13.9 a	52.9 a	0.28 a	0.28 a
Litter	12.4 ab	51.1 a	0.30 a	0.27 a
Duff	13.0 ab	54.4 a	0.31 a	0.27 a
Control (tap water)	11.7 b	49.6 a	0.28 a	0.26 a

¹Values followed by different letters are significantly different at the 5% level.

leaves and oak leaf leachates. Germinating seeds in fresh leaves represents an unnatural situation, because leaves in that state would never be a germination medium in the field. But, Experiment 1 was conducted to verify the occurrence of potential phytotoxins, perhaps even those not water soluble. Indeed, radicle growth was suppressed to its lowest level, averaging only about 50% of the control growth (table 1). Litter leachates reduced speed of germination in Experiment 2 (table 2); but seeds germinated very well on litter itself (table 1). The discrepancy might be explained by litter age. The litter used in Experiment 2 consisted of recently fallen leaves, whereas that used in Experiment 1 had been on the ground for 6 or 7 months. Incipient decomposition had taken place in the latter situation, possibly rendering the litter less toxic.

Simulated overwintering in oak leachates reduced radicle growth for both leaf treatments, and reduced germination speed in mature leaf and litter treatments. Again, fresh litter was used. As Rietveld (1979) points out, most plant chemical by-products probably are altered after reaching the soil. They likely are utilized and broken down by microorganisms, thus changed in form and in effectiveness. So, the leachates to which the seeds were exposed in the refrigerator may not be in the same form or concentration in the field.

Experiment 4, while conducted in a controlled environment, more closely approached natural forest conditions than the other experiments. Seeds germinated and seedlings grew in forest soils under diurnal temperature, relative humidity, and natural light fluctuations. Under these conditions, seedling emergence again was slowed by oak leaf leachates. However, seedling growth after 4 months was not reduced by any treatments. There are several reasons why growth suppression may not have been demonstrated under the conditions of this experiment. First, because the seedlings in each treatment that were allowed to grow for the entire 4 months were the first to germinate, all were approximately the same age. Therefore, the leachates apparently did not suppress shoot and root growth. However, growth differences resulting from slower

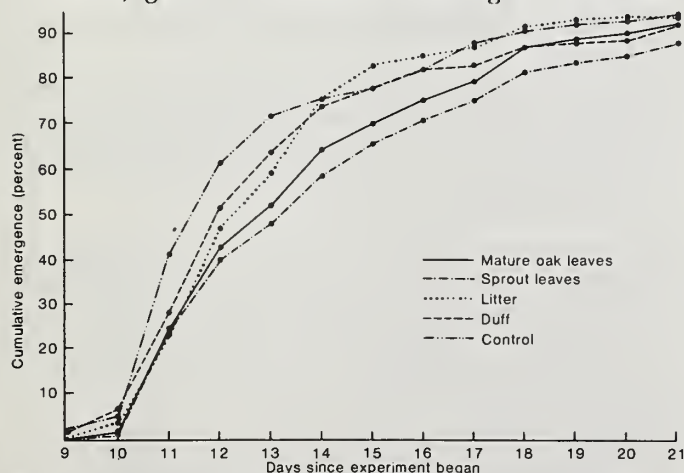


Figure 1.—Cumulative emergence (germination) of ponderosa pine seeds watered with Gambel oak leachates of mature leaves, sprout leaves, litter, duff, and tap water (control).

emergence and, therefore, shorter growing time were not allowed to be expressed. Second, although not measured, the leachates were likely nutrient-rich compared to the tap water used in the controls. So, growth of the control seedlings may have been somewhat depressed by nutrient deficiencies. Third, the first-year growing season for southwestern ponderosa pine is only about 2 months long. Therefore, any possible early growth reduction may have been overcome by the additional 2 months of this experiment. Fourth, the leachates in this experiment were prepared from air-dried leaves compared to fresh green leaves in the other experiments. Air drying may denature potential toxins and change their effectiveness shown in Experiments 1, 2, and 3.

The experiments reported here indicate that the freshest oak leaves produced the greatest toxicity. Green leaves of both mature oaks and sprouts slowed germination and early pine growth the most, while newly fallen oak litter caused greater reduction than litter which had overwintered. Well-decomposed oak duff produced no suppression of radicle growth.

Even though differences in germination rate and radicle growth between controls and oak leachate treatments were statistically significant, these differences, in some cases, do not initially appear to be great enough to cause regeneration failures in nature. However, these experiments were conducted under quite favorable temperature, moisture, and light conditions. In the forest, temperatures would be much more extreme at both ends, moisture would likely be limiting at some time, and light energy could be quite low. Therefore, under more normal field conditions, ponderosa seedlings presumably would be more susceptible to any potential phytotoxins. However, the leachates probably would be less concentrated in nature than in any of the experiments because of reduced efficiency of rain leaching compared to soaking. This could result in less toxicity, but again, seedlings would likely be more vulnerable.

It would be difficult to determine the amount and concentration of leachates in contact with pine seeds naturally. Concentration would vary greatly depending on oak canopy coverage, seedbed medium, and rainfall duration and intensity. Without this information and knowledge of possible binding or denaturing effects the soil components can have on potential phytotoxic leachates, it is difficult to judge the actual extent of allelopathic influences (Rietveld 1979); but, as mentioned, toxicity would likely be less than under experimental conditions. However, if oak by-products are naturally active, they probably are working with competition factors creating stresses in new pine seedlings surpassing those of either allelopathy or competition alone. Rietveld (1979) logically speculated that receiver species would be more susceptible to phytotoxins if they were already weakened by competition or, conversely, more susceptible to competition stresses if suppressed by phytotoxins.

With this in mind and knowledge of how natural ponderosa regeneration takes place in the Southwest, the possible nature of allelopathic action of Gambel oak on pine can be inferred. Ponderosa pine seed germination commences shortly after the summer rains begin, usually

in early July. Thus, seedlings have a maximum of 8 to 10 weeks to become established before fall (Schubert 1974). If germination is delayed and initial growth is slowed, seedling survival during the succeeding 9 harsh months is greatly reduced (Larson 1961). It seems possible that potential phytotoxins are leached from oak leaves during the summer rains and contact the pine seeds on the ground, slowing germination and/or initial root growth. In addition, the new seedlings are in competition for moisture with the established oaks, which are efficient water users (Tew 1969). Under these conditions, the pine seedlings are likely to be small, with poorly developed root systems going into the normally dry fall, or subsequent spring drought. Mortality undoubtedly would be high from desiccation or from frost-heaving of small-rooted seedlings. This situation of natural pine regeneration suppression resembles that described by Rietveld (1975) for ponderosa pine-bunchgrass communities of northern Arizona.

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Keywords: *Quercus gambelii*, *Pinus ponderosa*, natural regeneration, allelopathy.

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
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Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526